

# An ensemble high-resolution projection of changes in the future habitat of American lobster and sea scallop in the Northeast US continental shelf

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## Abstract

**Aim:** To address the uncertainty associated with climate-driven biogeographical changes in commercial fisheries species through an ensemble species distribution modelling (SDM) approach.

**Location:** Northeast US Continental Shelf Large Marine Ecosystem (NEUS-LME).

**Methods:** We combined an ensemble SDM platform (BIOMOD 2) and a high-resolution global climate model (NOAA GFDL CM2.6) to quantify spatiotemporal changes in habitat of two commercially important species in the Northeast US Continental Shelf Large Marine Ecosystem (NEUS-LME); American lobster (*Homarus americanus*); and sea scallop (*Placopecten magellanicus*). An ensemble SDM was calibrated using multi-decadal fisheries-independent surveys (1984–2016). Statistically weighted species-specific ensemble SDM outputs were combined with 80 years of projected bottom temperature and salinity changes in response to a high greenhouse gas emissions scenario (an annual 1% increase in atmospheric CO<sub>2</sub>).

**Results:** Statistically significant changes ( $p < .05$ ) in habitat suitability for both species were found over a large portion of the study area. Sea scallop undergoes a northward shift over the study period, while American lobster moves further offshore. The ensemble projections showed that several management zones were identified with increases and decreases in species-specific habitat. Uncertainty due to variations in ensemble member models was also found in the direction of change within each management zone.

**Main conclusions:** This study provides ensemble estimates of climate-driven changes and associated uncertainties in the biogeography of two economically important species in the United States. Projected climate change in the NEUS-LME will pose management challenges, and our ensemble projections provide useful information for climate-ready management of commercial fisheries.

Tanaka and Torre contributed equally and are listed alphabetically.

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## KEYWORDS

American lobster, BIOMOD, global climate model, Northeast US Shelf Large Marine Ecosystem, sea scallop

## 1 | INTRODUCTION

Species distribution and abundance are central components of ecological research and critical to both conservation planning and fisheries management (Franklin, 2010). The biogeography of many marine species is currently shifting in response to climate-related changes in water temperatures and other oceanographic conditions (Hollowed, Planque, & Loeng, 2013; Nye, Link, Hare, & Overholtz, 2009; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). Altered biogeography of a species poses several management challenges because changes in species distributions can move stocks in and out of fixed management boundaries (Gaines et al., 2018; Pinsky et al., 2018). Predicting responses of important fish stocks to future climatic conditions is critical to the implementation of adaptive management measures (Hollowed, Curchitser, Stock, & Zhang, 2013). However, likely shifts in biogeography for many species moving into the future remain largely unknown (Tompkins & Adger, 2004). Correlative species distribution models (SDMs), which rely on quantified species–environment relationships to explain and predict spatial distributions of species, have become important tools in adaptive natural resource management (Franklin, 2010). Long-term projections of species distribution shifts are often sensitive to complexities, properties and assumptions associated with an individual SDM algorithm (e.g. how much interaction among variables is considered or how a species' flexible responses along environmental gradients are fitted; Guisan, Thuiller, & Zimmermann, 2017). An emerging consensus recommends that uncertainty associated with climate-driven changes in species distribution can be better addressed through an ensemble SDM approach that can summarize and represent the information obtained across projections based on all SDMs considered (Gama, Crespo, Dolbeth, & Anastácio, 2016; Mędrzycki et al., 2017).

The Gulf of Maine (GOM), Georges Bank (GB), Mid-Atlantic Bight (MAB) and Southern New England (SNE) are parts of the Northeast US continental shelf Large Marine Ecosystem (NEUS-LME) (Townsend, Thomas, Mayer, Thomas, & Quinlan, 2006). Climate-driven changes in the GOM and GB ecosystem structure are a growing concern for its socio-economically important fisheries (Peck & Pinnegar, 2018). The NEUS-LME is undergoing rapid physical change with water temperature increased at an average of 0.04°C/year between 1982 and 2017 (Banzon, Smith, Chin, Liu, & Hankins, 2016; Reynolds et al., 2007; Figure S1). Recent studies showed a similar increasing trend in the GOM and GB fall water temperature during the period of 1968–2013, with faster warming rates in GB and the MAB (Kleisner et al., 2016, 2017). Furthermore, a recent high-resolution global climate model projection suggests that warming of the NEUS-LME associated with the radiative effects of greenhouse gases may be augmented by warming associated with dynamic shifts in the Gulf Stream associated with climate change (Saba et al., 2016). A projected

northerly shift in warm Gulf Stream waters may increase quantities of warm slope water entering the Northwest Atlantic Shelf, possibly leading to warming by as much as 4–5°C along the southern portion of the shelf (MAB and GB) and 3.7–3.9°C in the GOM along with an accompanying increase in salinity. Recent observations suggest that such a shift may be occurring (Caesar, Rahmstorf, Robinson, Feulner, & Saba, 2018).

American lobster (*Homarus americanus*; hereafter lobster) and sea scallop (*Placopecten magellanicus*; hereafter scallop) support two of the most economically valuable single-species commercial fisheries in the NEUS-LME with lobster valued at over 669 million USD and Scallop at over 486 million USD in 2016 (NMFS, 2016). These species are vital to the economies and social well-being of coastal communities in this area (NMFS, 2016). The biogeography of both American lobster and sea scallop is keenly affected by changes in climatic variables (Kurihara, 2008; Tanaka et al., 2018; Tanaka & Chen, 2016; Torre, Tanaka, & Chen, 2018, 2019). The latest benchmark assessment showed that the lobster stock in the southern range is severely depleted due to several environmental factors (e.g. climate-driven recruitment failure and shell disease; ASMFC, 2015). Recent studies also showed that observed and projected northern shifts in the distribution and habitat of American lobster (Greenan et al., 2019; Pinsky et al., 2013; Stanley et al., 2018). There have also been studies that have linked changes in the distribution of scallop in response to abiotic factors (benthic temperature, benthic salinity, bottom slope) and biotic factors (sea star predation; Lowen et al., 2019). Several species in the NEUS-LME are thought to be depleted due to a failure to recover from intense overfishing along with the southern extent of the species' range resulting from persistent warming conditions (Pershing et al., 2015; Wahle, Dellinger, Olszewski, & Jekielek, 2015). Therefore, long-term changes in the climate regime in the NEUS-LME are expected to greatly impact lobster and scallop habitat suitability (Caputi, Lestang, Flusher, & Wahle, 2013). Providing ensemble projections of climate-driven habitat suitability for these species is of great interest to stakeholders, policymakers and fishery management bodies.

While the effects of climate change are complex and diverse, the impacts on fisheries can be grouped into two general categories: changes to stock biomass or productivity, and changes to stock distribution, each of which poses different management challenges (Brander, 2009; Gaines et al., 2018). This study focuses on the latter, changes to stock distribution, which affects where fish can be caught and who has access to them over time. To evaluate potential climate change impacts on lobster and scallop fisheries, we considered bottom temperature and bottom salinity as proxies of species habitat suitability. These ecologically relevant and readily available variables have been shown to be

strong predictors of species distribution in recent modelling efforts (Kleisner et al., 2016; McHenry, Welch, Lester, & Saba, 2019; Rheuban, Kavanaugh, & Doney, 2017; Tanaka et al., 2018; Torre, Tanaka, & Chen, 2019). The objective of this study is to provide an ensemble projection, generated through a range of different SDMs, of the spatiotemporal changes in habitat of two most important commercial fish stocks in the NEUS-LME, lobster and scallop, in response to projected changes from the high-resolution climate model described by Saba et al. (2016). This study also provides a critical step towards establishing long-term adaptive management measures for lobster and scallop in the NEUS-LME.

## 2 | METHODS

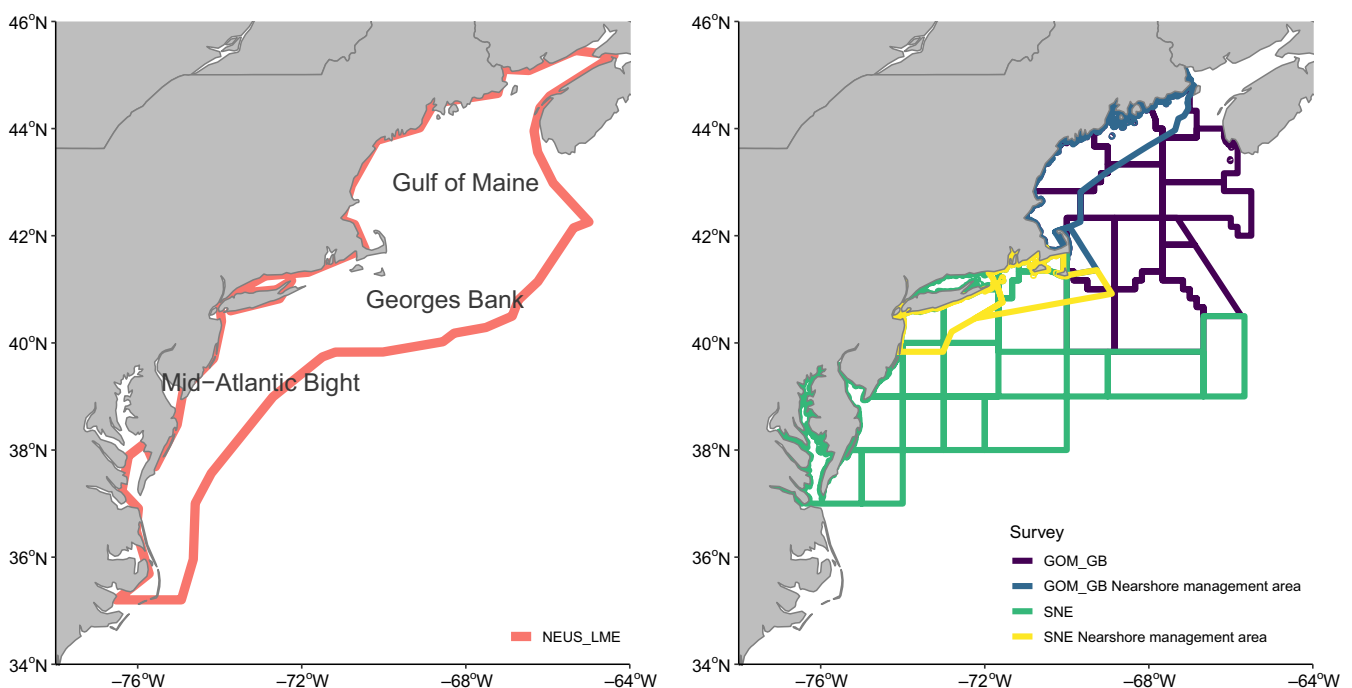
### 2.1 | Study area

This study area covers the majority of the NEUS-LME (38.0°–45.0°N and 75.0°–67°W; Figure 1). The NEUS-LME waters are encompassed by the Gulf Stream to the southeast and the U.S. coast to the northwest. These waters are comprised of mixed slope and shelf waters and can be divided into several relatively distinct regional sub-systems but are all interconnected to some degree by the Labrador Current which flows southward towards the equator (Townsend et al., 2006). This study was structured around important management zones for lobster and scallop (Figure 1) to incorporate a spatial scale relevant to management interests, as well as to encapsulate projected biological activity from each of these distinct subregions in the NEUS-LME.

### 2.2 | Study species

American lobster are large, mobile, cold-blooded, marine decapods and undergo migration to maintain exposure to optimal biophysical conditions (Caputi et al., 2013). American lobster are ectothermic and climate change can have a pervasive bottom-up influence throughout its larval and post-larval life stages (Caputi et al., 2013; Quinn, 2016; Steneck & Wahle, 2013). Water temperature has a significant impact on lobster's life history and ecology (e.g. recruitment, behaviour and distribution (ASMFC, 2015)). For example, the species undergo seasonal migrations likely regulated by temperature change as opposed to selecting for optimal habitat on an instantaneous basis. American lobster can be found spanning a range of temperatures, from –1 to 26°C (Quinn, 2016), while a preference for a narrower range, 12–18°C, and avoidance of temperature below 5°C and above 19°C has been demonstrated through laboratory experiments (Crossin, Al-Ayoub, Jury, Howell, & Watson, 1998). While the increase in water temperature may not negatively affect the availability of thermally suitable habitat, warmer temperature has been linked to the increased prevalence of epizootic shell disease, ESD caused by chitinolytic bacteria (Groner et al., 2016; Hovel & Wahle, 2010; Maynard et al., 2016).

Scallop are bivalve mollusks of the family Pectinidae. In contrast to lobsters, sea scallops are largely sedentary, especially during the adult phase of their life history (Shumway & Parsons, 2016). The species' abundance and distribution are influenced by a multitude of habitat characteristics and ocean currents that interact to control larval settlement and survival into the adult stage, whereas water temperature plays an important role in regulating the distribution of scallop



**FIGURE 1** Left: Spatial extent of the Northeast US continental shelf Large Marine Ecosystem (NEUS-LME). Right: Selected management areas within NEUS-LME; GOM\_GB (Gulf of Maine & Georges Bank), SNE (Southern New England)

through larval movement and post-larval survival/mortality (Hart & Chute, 2004; MacDonald & Thompson, 1985a, 1985b; Stokesbury & Himmelman, 1995; Thouzeau, Robert, & Smith, 1991; Wildish & Saulnier, 1992). Sea scallop occurs mainly at depths ranging from 15 to 110 m throughout its range but can be found in shallower water in the northern part of its range, where it has been reported at depths up to 2 m (Naidu & Anderson, 1984). Adults show optimal growth at a temperature between 10–15°C, with temperatures above 21°C being lethal, and prefer full-strength seawater ~35 ppt, with salinities of 16.5 ppt or lower being lethal (Stewart, 1994). Common predators for juvenile sea scallops in the NEUS-LME include the sea star (*Astropecten americanus*) and the rock crab (*Cancer* spp.). These species contribute significantly to scallop mortality and can thus impact their distribution and abundance (Hart, 2006).

## 2.3 | Survey data

The data available for the analysis are a multi-decade scientific bottom trawl survey dataset and associated environmental (bottom temperature, bottom salinity and depth) variables (Figure S2). The fishery-independent survey data of lobster and scallop were collected by the Northeast Fisheries Science Center (NEFSC: 1984–2016) that cover offshore continental shelf waters. For lobster, the Maine/New Hampshire (MENH: 2000–2016), Massachusetts (MA: 1984–2016), Rhode Island (10984–2016) and Connecticut (1984–2016) state survey data provided the additional coverage in the inshore waters (<3 nautical miles from shore; Figure S2). The inshore survey data were incorporated to address the known gap in the spatial coverage of lobster monitoring effort (Tanaka et al., 2019). The inshore trawl surveys and the NEFSC offshore survey were conducted during spring (April–June) and fall (October–December) of each year. Area coverage for the survey comprises the Western Scotian Shelf of the GOM, south to Cape Lookout, North Carolina. Briefly, these fishery-independent multispecies surveys are based on stratified random sampling design and target demersal fish and invertebrate species. In addition to catch data, environmental data are collected as well, with water temperature and salinity being measured at each station (NEFSC, 2018). Prior to the analysis, the survey data were screened to exclude surveys lacking key information (geographic coordinates, tow duration, date/year, bottom water temperature, salinity, depth and a number of species caught). This pre-analysis data screening process resulted in survey data containing 31,691 tows for lobster and 41,664 tows for scallop. For lobster, the total number of tows used in model calibrations is 31,691, which provided 19,847 absence and 11,844 presence records (37.37% presence). For scallop, the total number of tows used in the analysis was 41,664, which provided 23,744 absence and 17,920 presence records (43.01% presence). Lobster and scallop catches were standardized as numbers of each species caught in the survey specific area swept for the 20 min trawling (Table S1). More detailed information of these bottom trawl surveys is provided in the appendix, Johnston (2012), Politis, Galbraith, Kostovick, and Brown (2014) and Tanaka et al. (2019).

## 2.4 | Environmental information and climate projections

Projected oceanographic conditions used in this study were developed using the delta method (Fogarty, Incze, Hayhoe, Mountain, & Manning, 2008; Hare et al., 2012). The delta method is commonly used for future climate projection, which relies on the difference between future climate anomalies and a baseline regional climatology (historical climate condition). The delta method can remove the climate model projection biases (e.g. drift) and provide a simple and robust projection of future climate conditions (Hare et al., 2012).

The historical bottom temperature and salinity climatologies within the NEUS-LME were developed using high-resolution, quality-controlled monthly means from the Northwest Atlantic regional bottom temperature and salinity climatology for 1955–2012 (0.1°; Seidov et al., 2016) (Figure S3). Bathymetry data were obtained from the U.S. Coastal Relief Model (NGDC, 1999).

Projected bottom temperature and salinity conditions used in this modelling framework are from a high-resolution global climate model developed at the NOAA Geophysical Fluid Dynamics Laboratory (GFDL CM2.6; Delworth et al., 2012; Saba et al., 2016; Figures S4 and S5). CM2.6 is a coupled atmosphere-ocean-land-sea ice global climate model, with a 0.1° average horizontal resolution for its ocean component (Saba et al., 2016). CM2.6 resolves meso-scale oceanographic processes and fine-scale bathymetry within the NEUS-LME, leading to a better simulation of the regional ocean and shelf circulation when compared to global climate models with coarser ocean components (Saba et al., 2016). The monthly bottom temperature and salinity anomalies projections that correspond to spring and fall survey efforts were used in this study. The projected temperature and anomalies from CM2.6 are based on (a) the standard model initialization procedure where global atmospheric CO<sub>2</sub> is fixed at a 1,860 pre-industrial concentration to bring the climate system into near-equilibrium, and (b) a transient climate response to simulated 1% year<sup>-1</sup> increase in global atmospheric CO<sub>2</sub> run (i.e. 2xCO<sub>2</sub> simulation) up to 70 years and is then fixed for an additional 10 years. The CM2.6 2xCO<sub>2</sub> simulation can be roughly compared to the IPCC highest greenhouse gas emissions scenario (IPCC-RCP8.5). Under the IPCC RCP8.5 scenario, the global mean surface temperature increases by 2°C by 2060–2070 relative to the 1986–2005 climatology (Winton, Anderson, et al., 2014), whereas the CM2.6 2xCO<sub>2</sub> simulation projects the global mean temperature increases by 2°C by year 60–80. This results in bottom temperature warming on the scale of 1.8–2.9°C over the simulated 80 years across the NEUS-LMES.

## 2.5 | Ensemble species distribution modelling algorithm

Ensemble SDMs for lobster and scallop were calibrated using both presence-absence data and environmental data collected by the available bottom trawl survey programmes (Figure S2). The

environmental variables used for the ensemble lobster and scallop habitat modelling were directly obtained from the scientific bottom trawl survey dataset (1984–2016; Figure S2). We used bottom temperature, salinity and depth that were available at each tow location (Tanaka & Chen, 2016; Torre, Tanaka, & Chen, 2018). Furthermore, the location variables (i.e. latitude and longitude in decimal degrees) were used to capture the localized effects (Rooper, Zimmermann, Prescott, & Hermann, 2014; Tanaka, Belknap, Homola, & Chen, 2017; Tanaka et al., 2018; Winton, Wuenschel, & McBride, 2014). The data for modelling were from 31,691 for lobster and 41,664 tows for scallop. Environmental data used for the training of lobster models were matched directly to the specific time that the tow occurred, as this species has demonstrated behavioural and migratory responses to temperature (ASMFC, 2015; Caputi et al., 2013; Mercaldo-Allen & Kuropat, 1994). For sea scallop, dynamic environmental variables (bottom temperature and salinity) collected from the bottom trawl survey were averaged across all seasons. Temporal aggregation of these variables was carried out in order to incorporate the largely sedentary nature of this species and reflect an annual range of conditions from a given location (Torre et al., 2018). Potential collinearity among environmental variables used to predict species occurrence was assessed by calculating variance inflation factors (VIFs; Zuur, Ieno, & Smith, 2007). No predictor variable showed VIF value >3; therefore, the multicollinearity was assumed to be negligible.

Our ensemble SDM platform is based on the BIOMOD2 package developed in the R Programming environment (Thuiller, Georges, Engler, & Breiner, 2016). The BIOMOD2-based ensemble SDM algorithm can incorporate species presence–absence data and combine multiple SDM algorithms to provide robust species occurrence–environment relationships. The following 10 SDM algorithms were explored to predict spatiotemporal changes in presence probability of lobster and scallop across the study area under current (average 1955–2012 climatology) and future climatic conditions (CM2.6): generalized linear model (GLM), boosted regression tree (GBM), generalized additive model (GAM), classification tree analysis (CTA), artificial neural network (ANN), surface range envelope (SRE), flexible discriminant analysis (FDA), multiple adaptive regression splines (MARS), random forest (RF) and maximum entropy (Maxent). To optimize the fit to species' response curves and increase predictive performance from all SDM algorithms used in the ensemble modelling framework, a tuning process was developed where individual SDM parameters were varied using a 10-fold cross-validation procedure (Breiner, Nobis, Bergamini, & Guisan, 2018). For each algorithm, the SDM parameter setting yielding the highest receiver operator curve (ROC) value during the cross-validation procedure was kept (Table S2). For model tuning, the BIOMOD tuning function was used, which uses tuning functions from the CARET R-package to tune GBM, ANN, GAM, MARS, GLM and CTA (Kuhn, 2008), and ENMEVAL R-package to tune Maxent (Muscarella et al., 2014). 10-fold split sampling (90% training data and 10% test data) was used to evaluate the models.

Once SDMs were fitted with optimized parameters, all SDMs were run three times each using a randomly chosen 80% of the

presence–absence data, with the remaining 20% of the data being used to cross-validate model results. A balance of three runs per each SDM was struck to limit computational demands while still achieving stable results (Thuiller et al., 2016). Two SDM evaluation criteria, receiver operator curve (ROC) and the true skill statistic (TSS), were calculated through cross-validation and used to assess the performance of each algorithm, with higher values for each metric being an indication of higher model skill (Hill, Gallardo, & Terblanche, 2017; Mi, Huettmann, Guo, Han, & Wen, 2017). For both lobster and scallop, best-fitting SDM performance was evaluated against predetermined thresholds (TSS > 0.5 and ROC > 0.8; Hill et al., 2017; Mi et al., 2017). The built-in BIOMOD2 function was used to derive the relative predictor variable importance from the SDM runs that meet TSS and ROC thresholds with regard to structuring species distribution.

An ensemble SDM was built for each species using a composite of the SDM runs that meet predetermined TSS and ROC thresholds. Additionally, the response curves for all selected SDM outputs (response curves and spatial predictions) were visually assessed for validity. Top performing algorithms (excluding those with ecologically unrealistic results) were ranked by the TSS score and combined, using a weighted average of TSS scores, to produce the final ensemble model, which predicts the probability of presence for both lobster and scallop at 0.1° resolution across the study area. The weighted average of individual SDMs to form the final ensemble projection (FEP) was calculated as follows:

$$\text{FEP} = \frac{\sum_{i=1}^n A_i \times \text{TSS}_i}{\sum_{i=1}^n \text{TSS}_i} \quad (1)$$

where  $A_i$  denotes the habitat suitability (probability of presence) a single run of one of the 10 SDM algorithms;  $\text{TSS}_i$  denotes the true skill statistic score received by that run; and  $n$  is the total number of all runs of all algorithms to be included in the final ensemble model.

## 2.6 | Projections of future habitat

Weighted species-specific ensemble SDM was used to project habitat suitability of lobster and scallop across the NEUS-LME under historic bottom temperature and salinity conditions and over the future 80 years based on the transient climate-driven bottom temperature and salinity changes in response to the doubling of 1% CO<sub>2</sub> per year increase scenario applied in the NOAA GFDL CM2.6 (Saba et al., 2016). Future habitat projections are based on quantified response of lobster and scallop to changes in bottom temperature and salinity. Temperature and salinity were consistently identified as key proxies of changing climate (and water conditions) that were likely to influence the probability of species presence (Kleisner et al., 2017; McHenry et al., 2019; Tanaka et al., 2018, 2019; Torre et al., 2019). The regional bottom temperature and salinity climatology for 1955–2012 was used to project species-specific habitat suitability under the “current” conditions



(Figure S3). Species-specific habitat suitability change under future bottom temperature and salinity conditions were generated by combining the weighted ensemble SDM with the CM2.6 bottom temperature and salinity fields at every projected time step during the 80-year run (spring = March–May, fall = September–November, annual = spring & fall). Regression analysis was performed at every grid cell ( $0.1^\circ$ ,  $n = 10,497$ ), and the slope coefficient ( $\beta$ ) was used to detect a temporal trend in climate-driven habitat suitability during the projected 80 years.

Ensemble SDM outputs were further aggregated for each management zones (see Figure 1), and habitat suitability changes between the first and last 10 years of the projected 80 years were analysed for those economically relevant areas (GOM-GB and SNE nearshore areas) and areas spanning a gradient of oceanographic conditions (GOM-GB and SNE). First, proportional changes among each habitat suitability tercile (highly suitable  $>0.66$ , suitable  $0.33$ – $0.66$ , and least suitable  $<0.33$ ) within each management zone were analysed to detect any changes in the habitat space (i.e. changes in space occupied by a given habitat suitability tercile). Second, the two-sample Kolmogorov–Smirnov (KS; Conover, 1971; DeGroot & Schervish, 2002) test at the 95% level was employed to measure the degree of habitat suitability similarity between first and last 10 years of the 80-year projections. This nonparametric test is commonly used to compare two empirical continuous distribution functions. Habitat suitability values from the first 10 years (modelled years 1–10; 1st sample) and last 10 years (modelled year 71–80; 2nd sample) were treated as two empirical distributions at every projection grid across the study area ( $0.1^\circ$ ,  $n = 10,497$ ). The KS test was used to assess the null hypothesis that these two distributions are equal (e.g. grid-level KS estimates with  $p < .05$  indicating that the distribution of two habitat suitability samples from the first and last 10 years of the projected 80 years are significantly different).

## 2.7 | Assessment of uncertainty in the ensemble projections

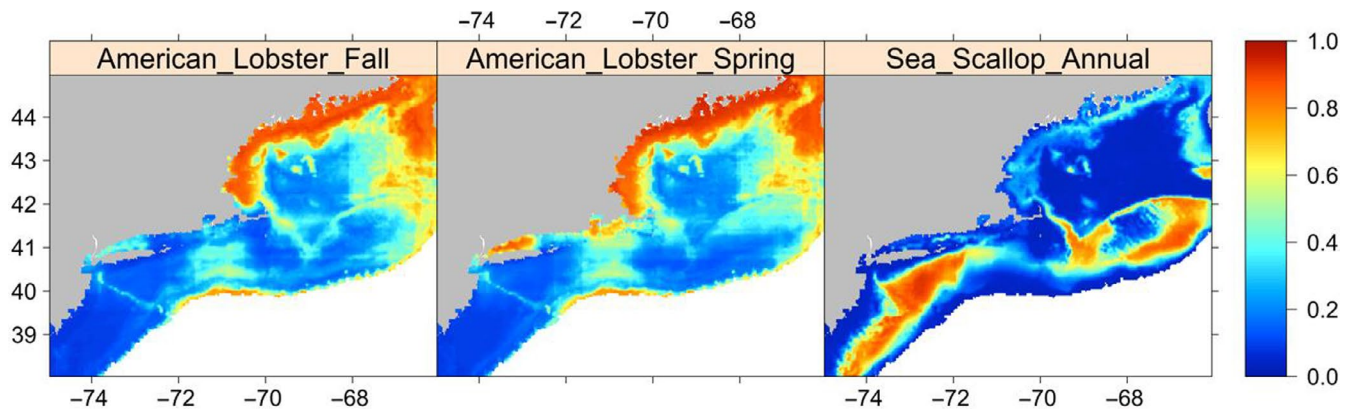
Finally, unanimity of agreement among individual ensemble members (i.e. every SDM run with  $TSS > 0.5$  and  $ROC > 0.8$ ) was analysed to assess the magnitude of uncertainty in the ensemble projections (Collins et al., 2013). A linear trend from every individual SDM projection was classified as either an increase (positive slope coefficient with  $p < .05$ ), decrease (negative slope coefficient with  $p < .05$ ) or no change ( $p \geq .05$ ). Agreement ratio among individual ensemble members was then calculated for each management area, where a ratio of 1 indicates that all individual SDM projections exhibited the same trend (increase, decrease or no change). The agreement ratio was calculated from both weighted and unweighted individual SDM projections. Unweighted agreement ratio indicated that all individual SDM projections were considered equally, while the weighted agreement ratio indicated that individual SDMs with higher skills were given more weight on agreement ratio. For a given management area, a projected trend was considered *likely* (agreement ratio above

66%) or *unlikely* (agreement ratio of less than 33%). Furthermore, the agreement ratio from both weighted and unweighted individual ensemble members was compared to assess the robustness of projected habitat suitability changes within each management area.

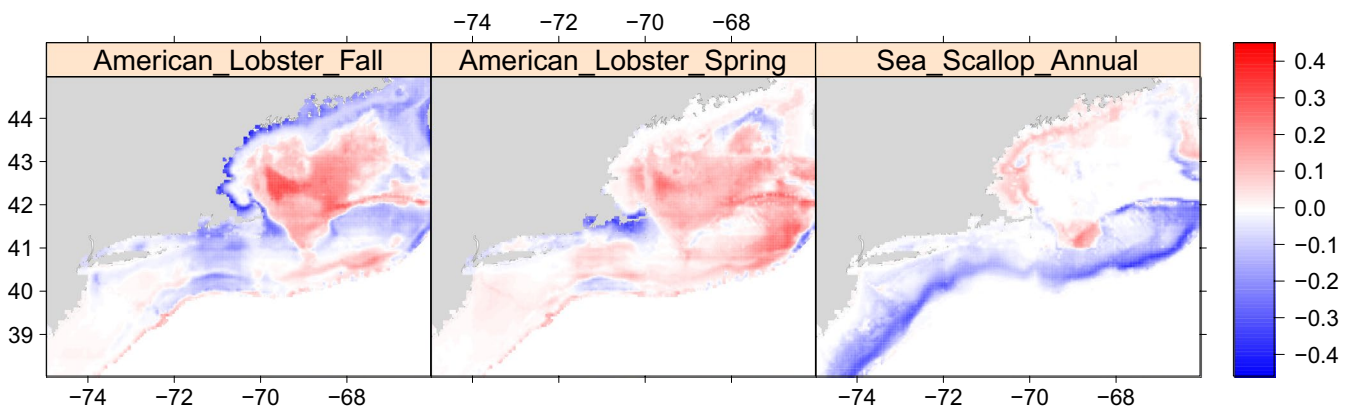
## 3 | RESULTS

For both lobster and scallop, 16 and 21 tuned SDM runs met the performance thresholds ( $TSS > 0.5$  and  $ROC > 0.8$ ; Table S3). ANN (2nd run), GLM (all runs), and SRE (all runs) did not meet the performance thresholds and were rejected for lobster, while GLM (all runs) and SRE (all runs) were rejected for scallop (Table S3). The prediction accuracies of the selected SDM runs for both lobster and scallop were considered acceptable by meeting both  $TSS > 0.5$  and  $ROC > 0.8$  thresholds (Tables S3 and S4). Additionally, based on spatially stratified cross-validation, we determine that both overfitting and spatial bias within our modelling framework are negligible (Figure S6). GBM showed the best performance and was highest weighted for both lobster and scallop (Figures S7 and S8). Response curves from the individual SDM algorithms included in final ensemble models indicated nonlinear relationships between the probability of presence and environmental variables for both species (Figures S9 and S10). For lobster, high agreement among selected SDM response curves was observed on bottom temperature, longitude and latitude. For scallop, response curves showed high variability on all predictor variables, suggesting their varying importance for driving the probability of the presence of this species. Latitude was the most important predictor variable in the lobster ensemble model, while the depth was the most important predictor variable in the scallop ensemble model. Bottom temperature was the most important dynamic predictor variable for lobster, while bottom salinity was the most important dynamic predictor variable for scallop (Figure S11).

The final ensemble model for lobster and scallop produced a spatial distribution of habitat that corresponds well to consensus of the general, broad-scale distribution of these species over the NEUS-LME (Figure 2). In general, a highly suitable habitat ( $>0.66$ ) for lobster was found along the inshore GOM up into the Bay of Fundy. During the spring, western Long Island Sound and the area south of Rhode Island showed high habitat suitability. For scallop, a highly suitable habitat ( $>0.66$ ) was found along offshore MAB, SNE and GB areas (Figure 2). Additionally, a highly suitable scallop habitat was found along the inshore GOM along with select offshore shoal areas. Projected warming across the NEUS-LME over the 80 years resulted in large spatial changes in habitat suitability of lobster and scallop (Figure 3). For lobster, deep areas within the GOM showed a strong increasing trend in habitat suitability. Lobster habitat suitability in inshore areas remained stable during the spring but showed a declining trend during the fall. The general distribution of changes in scallop habitat suitability over the study period showed a clear north-positive, south-negative trend (Figure 3), with habitat suitability declined in the MAB, SNE and GB areas. Within GOM-GB, inshore areas along with select shoal areas showed an increase in



**FIGURE 2** Maps showing the habitat suitability (probability of presence) for American lobster and sea scallop across the study area as predicted by the final ensemble model under the historical climatology (1955–2012). The colour ramp corresponds to predicted habitat suitability, where dark blue indicates low habitat suitability and red indicates high habitat suitability (scaled 0–1)



**FIGURE 3** Temporal change in habitat suitability (probability of presence) over the future 80 years of changes (linear trend per 80 years) in bottom temperature and salinity for American lobster and sea scallop. The colour ramp corresponds to a linear trend in habitat suitability with red areas having a positive change and blue areas having a negative change

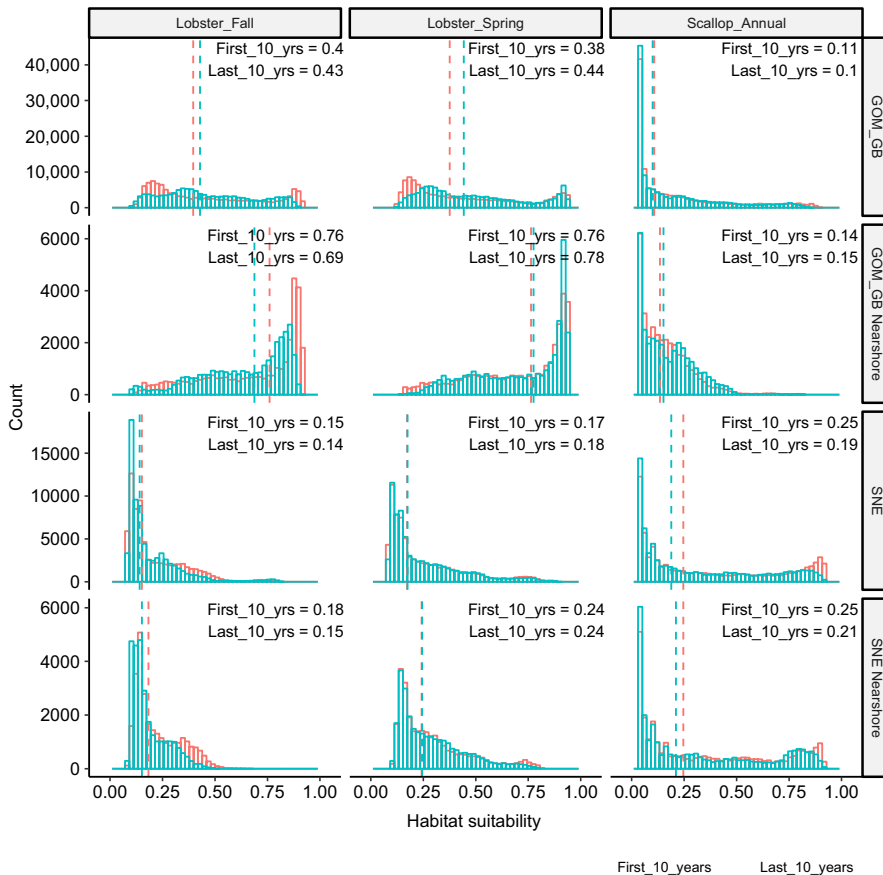
scallop habitat suitability while deeper offshore areas remained relatively stable.

Changes in habitat suitability between the first and last 10 years of the projected 80 years were aggregated within each management zone. For lobster, a decline in the highly suitable habitat (habitat suitability tercile  $>0.66$ ) was found in the GOM-GB nearshore area during the fall ( $-6.89\%$ ), while both of the SNE areas during the fall showed an increase in the area occupied by the least suitable habitat (habitat suitability tercile  $<0.33$ ) ( $+12.66\%$  for SNE,  $+23.68\%$  for the SNE nearshore) (Figure S10). For scallop, the SNE area showed a decline in the space occupied by the highly suitable habitat ( $-19.23\%$ ), and the GOM-GB nearshore area showed a decline in space occupied by the least suitable habitat ( $-5.38\%$ ) (Figure S12).

For lobster, most of the statistically significant habitat suitability changes ( $p < .05$ ) were associated with deeper areas within the GOM-GB area during both seasons, and also the majority of the GOM nearshore area during the fall (Figures S13 and S14). In contrast, Sea scallop exhibited statistically significant changes in habitat suitability over a large portion of the study area ( $>60\%$ ) (Figures S13 and S14). For lobster, major changes in median habitat suitability were from spring GOM-GB (first 10 years = 0.38, last

10 years = 0.44) and fall GOM-GB nearshore (first 10 years = 0.76, last 10 years = 0.69; Figure 4). Suitable scallop habitats decreased throughout SNE (first 10 years = 0.25, last 10 years = 0.19 for nearshore, first 10 years = 0.25, last 10 years = 0.21 for whole area; Figure 4).

80 years of ensemble projections within management zones were associated with statistically significant ( $p < .01$ ) changes in species habitat suitability (Figure 5 and Table 1). For lobster, habitat suitability in the SNE management areas was projected to decrease during the fall, while the GOM-GB management areas showed an increasing trend except for the GOM-GB nearshore area during fall. For scallop, only the GOM-GB nearshore area showed an increasing trend in the species' habitat suitability. Internal variability in the ensemble habitat suitability projections indicated that individual SDM predictions exhibited a range of trends (increase, decrease or no change) within each management area (Figure 5). Variability among the individual SDMs often increased as the model year progressed (e.g. lobster habitat suitability projections in the fall GOM-GB management area). Several management areas were associated with a high agreement ratio for projected changes in species habitat suitability (Table 2). For lobster, the projected decline in habitat suitability in



**FIGURE 4** Spatially aggregated changes in habitat suitability for American lobster and sea scallop between first and last 10 years under the future 80 years of changes in bottom temperature and salinity within selected management zones. Vertical dotted lines represent median from each time period. Median habitat suitability values from each period are shown within each panel. GBK, Georges Bank; GOM, Gulf of Maine; SNE, Southern New England

the GOM-GB nearshore and SNE management areas during fall were considered *likely* (i.e. at least 66% of the individual SDMs agreed on a statistically significant declining trend), while the projected increase in lobster habitat suitability in the GOM-GB during spring was *likely*. For scallop, both weighted and unweighted agreement ratios among individual SDMs indicated *likely* decline in scallop habitat suitability within the SNE management areas.

## 4 | DISCUSSION

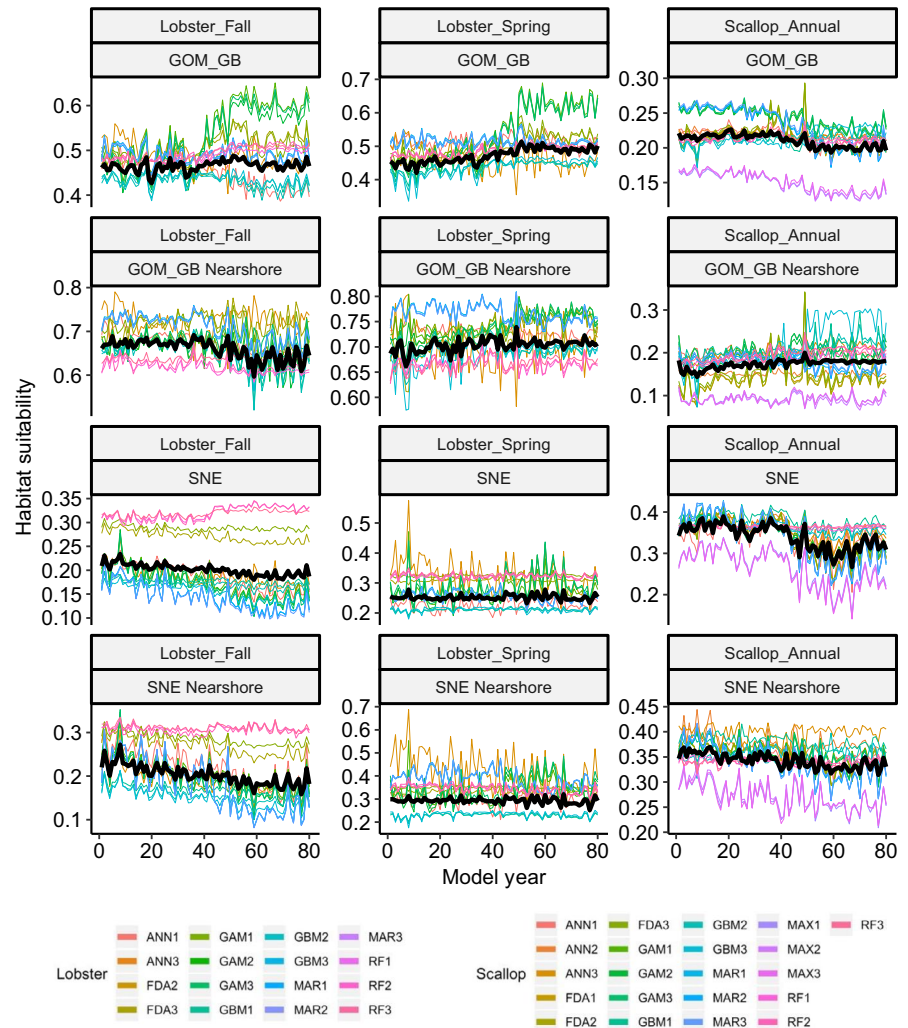
Ensemble SDMs are increasingly being used in ecology as they address a major challenge associated with SDM algorithm selection, that can have a large impact on projections (Araújo & New, 2007; Buisson, Thuiller, Casajus, Lek, & Grenouillet, 2010; Forester, Dechaine, & Bunn, 2013). Studies have shown that projections based on a single SDM, out of the myriad biostatistical approaches currently available, can have enough variability to cause misinterpretation of even a simple application (Araújo & Luoto, 2007; Pearson et al., 2006). For example, Pearson et al. (2006) applied nine commonly used bioclimatic models to a standardized dataset on South African plant species and found widely ranging results among different modelling techniques. Such challenge constitutes a large source of uncertainty in SDM outputs; however, a growing body of literature suggests that the combination of individual algorithms yield lower mean error than any individual constituent part (Araújo &

New, 2007; Buisson et al., 2010). Through providing a method to alleviate issues associated with variability in ecological predictions across a wide range of currently available statistical methods, ensemble SDMs provide the distinct advantages of offering a more straightforward approach to model selection. Our ensemble modelling procedure that weights each model according to its predictive performance can minimize the bias associated with a particular modelling approach. These are important considerations because the rapidly changing NEUS-LME requires more robust SDM modelling efforts.

This study provided an ecosystem-wide projection of lobster and scallop habitat suitability changes in response to simulated 1% year<sup>-1</sup> increase in global atmospheric CO<sub>2</sub> concentration, which was characterized by more than 1°C increase in the average bottom temperature in the areas of high lobster and scallop abundance (Figure S4). For lobster, the key findings include a marked decrease in fall inshore habitat suitability and a statistically significant increasing trend in habitat suitability in the deeper GOM-GB area (Figure 5 and Table. 1). Only offshore GOM-GB areas were identified as the area with an increasing trend in habitat. Temperature-driven habitat shifts towards deeper offshore also suggest a potential decrease in the probable distribution of lobster in the fall. The dominant temporal trend for scallop over the simulated 80 years is a climate-driven habitat reduction in every management area except for the GOM-GB nearshore area. While these changes would not move a broad spatial summary between habitat suitability tercile classifications (highly



**FIGURE 5** Changes in habitat suitability (probability of presence) over the future 80 years for American lobster and sea scallop in the selected management areas. Individual projections (thin coloured lines) for each habitat model; weighted ensemble mean (thick black line) for all habitat models. GB, Georges Bank; GOM, Gulf of Maine; SNE, Southern New England. ANN, artificial neural network; FDA, flexible discriminant analysis; GAM, generalized additive model; GBM, generalized boosting model; MARS, multiple adaptive regression splines; MAX, maximum entropy; RF, random forest



suitable >0.66, suitable 0.33–0.66, and least suitable <0.33) as habitat generally remained within the coarse tercile groupings, this study suggests that climate change will act as a likely stressor to the southern lobster and scallop fisheries and continues to drive the further contraction of scallop and lobster habitats into the northern areas. These findings parallel other studies on the spatial distribution of these species in response to oceanographic change in the Northwest Atlantic (Howell, 2012; Stanley et al., 2018; Steneck & Wahle, 2013; Tanaka & Chen, 2016; Torre et al., 2018; Wahle, Castro, Tully, Cobb, & Cobb, 2013). Similar findings were also reported for other major commercial stocks in this region. Nye et al. (2009), analysed temporal trends of the centre of biomass, mean depth, mean temperature of occurrence and area occupied of 36 fish stocks from 1968 to 2007 and found that many stocks exhibited a poleward shift with a concurrent increase in depth.

We analysed the ratio of agreement between individual model projections to provide a useful measure of uncertainty in the species habitat suitability projections (Table 2). Assessment of individual SDM agreement in habitat suitability trend identified management areas with robust changes, areas with small changes or areas where models disagree or a combination of those. Statistically weighted ensemble means generally offers a more useful estimate of changes

in species habitat suitability distribution as it is less sensitive to outliers. The trends in the ensemble habitat suitability projections were statistically significant in 10 out of 12 management areas (Table 2). However, we showed that there were significant differences between the different members of the final ensemble projections (Figure 5), and it is important to note that the ensemble means do not always imply robustness of species response across individual SDMs. For example, the statistically significant increasing trend in the spring lobster habitat suitability within the GOM-GB nearshore management area was associated with a large uncertainty, as the agreement ratio among individual SDMs was between 39%–44% (generally interpreted as “about as likely as not”; Collins et al., 2013). Similarly, we were able to detect relatively large internal variability (i.e. disparity in agreement ratios from weighted and unweighted ensemble projections) in the scallop habitat projections in the GOM-GB management areas (Table 2). It is important to acknowledge that these assessments do not necessarily reduce uncertainty in the ensemble projections and confidence statements cannot be inferred from model agreement alone. However, we recommend the assessment of agreement between individual ensemble members as a measure of uncertainty in the ensemble projections (Collins et al., 2013).

**TABLE 1** Linear trends in the ensemble habitat suitability projections by species, season and management area

Species	Season	Management area	Slope	p-value
American lobster ( <i>Homarus americanus</i> )	Fall	GOM_GB	0.01	<.01
		GOM_GB Nearshore	-0.03	<.001
		SNE	-0.03	<.001
		SNE Nearshore	-0.03	<.001
	Spring	GOM_GB	0.04	<.001
		GOM_GB Nearshore	0.02	<.001
		SNE	0	.94
		SNE Nearshore	-0.01	.09
Sea scallop ( <i>Placopecten magellanicus</i> )	Annual	GOM_GB	-0.03	<.001
		GOM_GB Nearshore	0.03	<.001
		SNE	-0.03	<.001
		SNE Nearshore	-0.03	<.001

Abbreviations: GB, Georges Bank; GOM, Gulf of Maine; SNE, Southern New England.

Modelled habitat suitability in this study should be interpreted as a proxy for probability of presence (occupancy) as opposed to actual lobster and scallop habitat suitability, given that measured catch was affected by some niche dimensions and processes not explicitly included in the predictors (e.g. territorial occupancy occurring at smaller scales) (Tanaka et al., 2018; Torre et al., 2018). Furthermore, projected species habitat suitability changes in this study should be viewed as a potential change in occupancy of a species due to changes in bottom temperature and salinity while holding all other top-down and bottom-up variables constant (e.g. fishing pressure and species interaction), and long-term habitat suitability changes for both species are likely not unanimously linked to the large-scale warming. For example, the assessment of variable importance revealed bottom salinity to be the most important climatic variable for scallop (Figure S7), indicating that multi-decadal variability of the scallop habitat availability across the NEUS-LME was primarily driven by changes in bottom salinity (Figure S11). Salinity is a physiologically important environmental variable for marine species, and it can directly influence broad-scale species distribution patterns in nearshore waters and estuaries (e.g. lobsters in Long Island Sound; Tanaka & Chen, 2015; Watson III, Vetrov, & Howell, 1999). For scallop, as large portions of the study area are well within the species' physiological tolerance (29.9–35.6 ppt), the observed scallop–salinity relationship is likely related to other variables that are structured along salinity gradients in a given area (e.g. origin of water mass; Torre et al., 2019). As is often the case with species–environment modelling, certain variables may be functioning as surrogates for factors directly controlling species distribution through physiological mechanisms (Araújo & Peterson, 2012; Austin, 2007). Regional predator–prey interactions such as sea star predation on sea scallops can also have a significant effect on the distribution of the species at smaller scales (Hart, 2006; Hart & Chute, 2004; Lowen et al., 2019). Furthermore, we used latitude and longitude as proxy variables to capture a wide range of covarying bio-climate factors such as spatiotemporally variable fishing pressure and larval supply (Guernier, Hochberg, & Guégan, 2004;

Shumway & Parsons, 2016; Tanaka et al., 2018; Wikgren, Kite-Powell, & Kraus, 2014). As a result, certain areas with high-quality habitats may have a lower probability of detected presence. Another potential limitation of our modelling approach is that the interpolation of survey-derived environmental data masks the scale at which fine-scale habitat selection (active or passive) is occurring for each species. These are important points to consider in future studies. This study focused on evaluating the changing species habitat suitability over large a large spatial scale. Our dataset reflects more than 30 years of aggregated species occurrence–environment relationship characterized by broad spatial and temporal ecological ranges, which can reduce uncertainty in the subsequent projection effort by allowing models to incorporate more complete species' realized niche. As more comprehensive environmental data becomes available in the future, a further detailed ensemble SDM approach could include additional variables such as pH, dissolved oxygen, predator–prey and other food–web interactions to capture a more comprehensive representation of the biogeography of lobster and scallop (e.g. Bio-ORACLE <http://www.bio-oracle.org/>).

Our study can contribute to the assessment of exploited fishery resources in a rapidly changing environments such as the NEUS-LME. For example, our study can contribute to lobster and scallop assessment by improving the effectiveness of survey efforts and the precision of stock assessment models. Fishery-independent surveys are a critical component of stock assessment as they provide spatial and temporal information about lobster and scallop stocks (ASMFC, 2015; Johnson et al., 2015). However, the effectiveness of the survey depends greatly on both the bias and precision of abundance estimates (Mier & Picquelle, 2008), and geographically uneven change in lobster and scallop catch could lead to inefficient survey design and the allocation of sampling effort. Even when intensive sampling efforts are conducted, resource limitations often preclude the acquisition of adequate spatial or temporal coverage to capture an entire range of available habitat, or species distribution, which

**TABLE 2** Weighted and unweighted agreement ratio for projected habitat suitability changes over the future 80 years. A linear trend from every individual ensemble member SDM projection was classified as either an increase (positive slope with  $p < .05$ ), decrease (negative slope coefficient with  $p < .05$ ) or no change ( $p \geq .05$ ). Agreement ratio of 1 indicates that all individual SDM projections exhibited the same trend (increase, decrease or no change). Unweighted agreement ratio indicates that all individual SDM projections were considered equally, while the weighted agreement ratio indicates that individual SDMs with higher skills were given more weights on agreement ratio (assigned weights are shown in Figure S2). Number of accepted model runs; lobster ( $n = 16$ ), scallop ( $n = 21$ )

Species	Season	Management area	Increase		Decrease		No change	
			Unweighted	Weighted	Unweighted	Weighted	Unweighted	Weighted
American lobster	Fall	GOM_GB	0.50	0.36	0.38	0.47	0.13	0.16
		GOM_GB Nearshore	0.06	0.01	0.75	0.84	0.19	0.15
		SNE	0.19	0.20	0.81	0.80	0.00	0.00
		SNE Nearshore	0.00	0.00	0.88	0.86	0.13	0.14
	Spring	GOM_GB	0.69	0.87	0.06	0.04	0.25	0.09
		GOM_GB Nearshore	0.44	0.39	0.25	0.09	0.31	0.52
		SNE	0.25	0.24	0.25	0.04	0.50	0.71
		SNE Nearshore	0.19	0.13	0.44	0.24	0.38	0.63
Sea scallop	Annual	GOM_GB	0.10	0.21	0.81	0.57	0.10	0.22
		GOM_GB Nearshore	0.48	0.81	0.14	0.00	0.38	0.19
		SNE	0.00	0.00	0.90	0.80	0.10	0.20
		SNE Nearshore	0.10	0.22	0.81	0.66	0.10	0.12

Abbreviations: GB, Georges Bank; GOM, Gulf of Maine; SDM, Species Distribution Models; SNE, Southern New England.

can result in under-informed management decisions (Brown, Buja, Jury, Monaco, & Banner, 2000). Here, developing a species-specific ensemble habitat projection with a magnitude of uncertainty provides several advantages in avoiding fixed and subjective stratification to improve the precision and accuracy of estimated stock status (Shelton, Thorson, Ward, & Feist, 2014). Additionally, many stock assessments fail to incorporate long-term changes to species distribution (NMFS, 2010; Skern-Mauritzen et al., 2015), highlighting the need for model projections of spatiotemporal changes to fish stocks. In the traditional stock assessment models that focus on the context of commercial fishing, natural mortality is often relegated to a single, typically time-invariant parameter that is not related to the species' ecology (ASMFC, 2015; Johnson et al., 2015). Incorporating climate-driven habitat availability into stock assessments may also improve the model fittings by defining different modelling time periods with respect to these processes (Tanaka et al., 2019). One accomplishment of this study is to provide an ensemble projection of the future habitat availability of the lobster fisheries by synthesizing multiple surveys (Figure 3). Several studies have documented the climatic impact on the species' biogeography (e.g. Kleisner et al., 2017; Pinsky et al., 2013) based on the offshore survey data alone, which does not cover the inshore waters where over 95% of lobster catches were reported (e.g. Maine, New Hampshire and Massachusetts; Tanaka et al., 2019). Multiple survey data can calibrate SDMs with better inputs and, therefore, allow these models to make more reliable species preference functions and predictions as well as reasonable spatial coverage of the area relevant to the management of this species.

Commercial marine fisheries are complex socio-ecological systems that support social well-being and global food security (FAO, 2018). The ecological, economic and social value of fisheries depends largely on the biomass of fish stocks, with fishing pressure being the main driver of resource status (Hilborn & Walters, 1992). Species distributions are influenced by many interacting biotic and abiotic processes, which can manifest as highly unpredictable occurrence–environment relationships (Boulangeat, Gravel, & Thuiller, 2012; Merow et al., 2014). While there are numerous examples of climate-forced distribution shifts, there has been little progress incorporating population regime changes into stock assessments and management outputs (Link, Nye, & Hare, 2011; Smith, Sameoto, & Brown, 2017). Changes in stock distribution pose several management and conservation challenges because it can affect the traditional boundaries principles for sustainable governance of common-pool resources (e.g. catch allocations based on historical stock availabilities within existing management boundaries; Pinsky et al., 2018). Current management practices are generally focused on maintaining fisheries stock biomass or productivity within fixed management boundaries and have accorded little considerations to environmental factors (Pinsky et al., 2018; Skern-Mauritzen et al., 2015). However, there are some studies that have provided useful examples of efforts to incorporate climate-forced distribution shifts into stock assessments. For example, Link et al. (2011) outlined a decision tree framework for addressing stock distribution shifts, with approaches falling into one of three categories: re-evaluate stock identification, re-evaluate a stock unit area or implement spatially explicit modelling. Additionally, Smith et al. (2017) discuss the

application of a spatial model for fishing effort to the state-space Bayesian stock assessment model for the Canadian maritime sea scallop fishery to incorporate habitat associations with both population processes and spatial fishing patterns. These examples demonstrate that while the effects of climate change are complex and diverse, decision-making beyond the traditional boundaries principles should use as much information and knowledge as possible to maximize the benefits of management actions and subsequent policy implementations (De Ornellas, Milner-Gulland, & Nicholson, 2011). The first step is for management authorities to identify areas of biogeographical changes with reliable projections and associated uncertainties and establish adaptive management strategies to cope with fisheries impacted by ecosystem change. For example, our ensemble future habitat projections with uncertainty estimates can increase the long-term effectiveness of marine protected areas and spatially explicit catch quotas to reduce pressures on fish stocks that are expected to experience further habitat degradation. Responding to biogeographical changes in natural resources requires a tool that can synthesize large amounts of information and policies that are appropriately adaptive and adequately informed by high-quality projections.

Our study proposed an ensemble means to infer the potential future habitats, based on high-resolution climate data, of two economically important fisheries resources in the NEUS-LME. Through providing a method to alleviate issues associated with variability in ecological predictions across a wide range of currently available SDMs, ensemble modelling approaches provide the distinct advantages of reducing error in projections and providing a more reliable estimate of uncertainty (Araújo & New, 2007; Buisson et al., 2010). Additionally, the use of geographically comprehensive survey data can reduce bias in the subsequent modelling efforts. Thus, the modelling framework developed in this study adds quality projections of spatiotemporal trends in the distribution of lobster and scallop, which constitute a critical step to improving the management of these species.

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## DATA AVAILABILITY STATEMENT

Both the field survey data and climate model output used in this study were provided by third parties. While we are not able to share the data and model output provided to us, all sources used in this study are available upon request from the following contacts; 1. The bottom trawl survey data were collected by the Atlantic States Marine Fisheries Commission (State survey data) and the NOAA Northeast Fisheries Science Center (Federal survey data), which may

be contacted at [jkippp@asmfc.org](mailto:jkippp@asmfc.org) and [james.manning@noaa.gov](mailto:james.manning@noaa.gov); 2. Bottom temperature and salinity output from NOAA GFDL's CM2.6 global climate model, please contact [vincent.saba@noaa.gov](mailto:vincent.saba@noaa.gov).

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#### BIOSKETCH

Our research focus includes ensemble projections of climate impacts on living marine resources, fisheries stock assessments, spatiotemporal models and use of multi-annual to decadal environmental predictions for marine resource applications.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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